

## SPECIAL FEATURE – EDITORIAL

### FACILITATION IN PLANT COMMUNITIES

# Facilitation in the conceptual melting pot

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## Summary

1. Here we present an introduction to this issue's Special Feature arising from the British Ecological Society Symposium: Facilitation in Plant Communities (20–22 April 2009).
2. Papers in the Special Feature demonstrate the benefits that arise from cross-system application of general concepts, for example, the well-known stress gradient hypothesis. Such comparisons challenge our definition of facilitation, as well as our pre-conceptions on the nature of intermediary organisms.
3. We suggest that under some circumstances a clear definition of the two-way nature of interactions is essential, e.g. when considering the evolutionary implications of facilitation. In other cases, however, we can perhaps be more relaxed, e.g. when facilitation is a component of conservation ecology.
4. *Synthesis.* Overall we believe that establishing facilitation as an independent concept has driven substantial progress towards a clearer understanding of how ecological systems work. Through the links established by work such as that presented in this Special Feature, we believe this field will continue to make rapid progress and aid ecological understanding in general.

**Key-words:** competition, facilitation, mutualism, parasitism, plant–plant interactions, soil organisms, synthesis, trophic interactions

## Introduction

Facilitative interactions, i.e. beneficial interactions among plants, are receiving increasing attention in plant ecology. Recently, perhaps buoyed by this increased interest, the pool of researchers addressing this topic has started to come together as a research community. In 2007, a European Science Foundation-funded workshop 'Facilitation, Biodiversity, Invasibility in a Changing World', held at the University of Bordeaux's Marine Biological Station, Arcachon, France, led to the production of a substantial essay review on the role of facilitation in plant communities (Brooker *et al.* 2008). This review looked at the progress made in the study of facilitation in plant communities, and the integration of facilitation into other areas of ecology. It also identified areas of potential future research, discussing under-exploited links to topics of clear relevance (e.g. ecological modelling, plant evolution).

The 2009 British Ecological Society Symposium: Facilitation in Plant Communities (20–22 April 2009, University of

Aberdeen, Scotland, UK) gave researchers interested in facilitation the chance to address these issues – to actively develop conceptual links with other research areas from which research on facilitation might gain and to which, hopefully, research on facilitation might contribute. The meeting provided an opportunity to recap the most current research on facilitation. But rather than populating the programme entirely with well-known faces from this research area and continuing well-worked discussions – e.g. the debate concerning the stress gradient hypothesis (SGH; see most recently Maestre *et al.* 2009) – the Symposium featured speakers who did not normally focus on plant–plant facilitation and thus created explicit links with the conceptual areas identified by Brooker *et al.* (2008) as promising targets for synergistic research. The meeting also provided a platform for the presentation of high-quality research by early-career scientists.

Participants were given the additional opportunity to publish output from the Symposium as a Special Feature in this issue of *Journal of Ecology*. Our aim in this introduction to the Special Feature is to summarize the recurring themes and key messages within this wide-reaching set of papers, and to provide a synthesis of the overarching research ideas and pathways that stem from them.

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### Cross-system comparisons raise some tricky issues...

Cross-discipline or cross-environment comparisons are essential for developing general models of ecology and for forcing us to think carefully about ideas that have developed concerning any ecological process. Several papers in the Special Feature take the opportunity to consider facilitation beyond the direct – or well-known indirect (e.g. grazer-mediated) – facilitative interactions in plant communities.

The paper by Bulleri (2009), for example, addresses the role of facilitative interactions in coastal marine environments and draws parallels between marine and terrestrial plant systems. This highlights a surprising fact – that facilitation research is perhaps not as well developed in marine biology as it is in terrestrial plant-community ecology. This is despite the fact that some of the key studies driving the development of facilitation research in plant communities have come – at least in part – from marine or coastal systems (e.g. Connell & Slatyer 1977; Bertness & Callaway 1994; Bruno, Stachowicz & Bertness 2003). Bulleri explores the possibility of adapting theoretical frameworks such as the SGH for marine facilitation research, specifically testing the cross-system validity of this concept. In a review of facilitation research in marine systems, he finds that facilitation in response to consumer pressure is more frequently found in less severe subtidal habitats. This clearly matches the model proposed by Bertness & Callaway (1994) wherein the role of consumer pressure in driving facilitative interactions increases in less abiotically severe environments. Bulleri's work makes us think about how we define facilitation: must benefactor and beneficiary species belong to the same trophic levels? Bulleri concludes that in marine systems, where organisms at different trophic levels are almost as spatially static as terrestrial plants, benefactors and beneficiaries frequently belong to different trophic levels. This is in contrast to the plant-centric focus (Callaway 2007; Brooker, Maestre & Callaway 2008) which emphasizes 'those positive, *non-trophic* [our emphasis] interactions that occur between physiologically independent plants and that are mediated through changes in the abiotic environment or through other organisms'. Bulleri concludes that the prevalence of facilitation between trophic levels in marine systems has clear implications for the applicability of the SGH in marine systems – particularly at the extreme ends of environmental gradients – given the low level of resource niche overlap that we might expect between species from different trophic levels.

Discussion during the Symposium clearly indicated some unease concerning the expansion of the facilitation concept to encompass cross-trophic level interactions. In other words, we usually use the terms 'predation' or 'parasitism' to identify trophic interactions in which a 'beneficiary' gains from eating a 'benefactor'. However, this challenge to our working definition of facilitation, and the specific need *in some circumstances* to clarify it, is evident in a number of the articles in this Special Feature. A related theme is the role of third-party organisms in mediating facilitative interactions, which likewise challenges some of our current definitions. As mentioned, in the marine

environments discussed by Bulleri, such mediation is often associated with consumer pressure: only by the mediating presence of the consumer does a beneficial interaction (either within or across trophic levels) operate. Consumer (grazer) mediated indirect competition in plant communities is common. However, despite the potential scale of their impacts, the facilitative indirect effects of soil biota are only just beginning to move onto the radar of facilitation research, even though there is a rich literature on this topic. Specifically Van der Putten (2009), in a discussion of the role of soil-borne pathogens in mediating plant–plant interactions, demonstrates, using the example of the dune grass *Ammophila arenaria*, how the impact of pathogenic soil microbes on this dominant species can turn it from competitor into a facilitator. This facilitation process is important in preventing the species from being permanently dominant – in areas without soil pathogens that can effectively restrict *A. arenaria*, the grass becomes both dominant and invasive. In a similar vein, Van der Heijden & Horton's (2009) review examines the mediating role of another group of soil organisms, namely mycorrhizal fungi. They also find evidence of context-specificity for the nature of their mediation. For example, they examine the impact of mycorrhizal fungal networks on the establishment and growth of seedlings in the presence of adult plants. The responses of seedlings were highly variable and dependent, e.g. on the availability of soil nutrients and the mycorrhizal characteristics of potential benefactor species.

The theme of context-specificity is reiterated by Watson (2009), although he also challenges our working definition of facilitation. He starts by reminding us of a key review by Press (1998) of the ecological function of parasitic plants. This review provocatively asked the question: Are they Dracula or Robin Hood? Watson's work returns to this issue, looking at the impact of parasitic plants at a range of scales, assessing whether their net effects are beneficial or detrimental. Through mechanisms such as the deposition of nutrient-rich litter and the attraction of pollinators by increasing local flower densities, parasitic plants can have beneficial impacts on their host. Moving beyond the host species, they can also have beneficial impacts on other plants, e.g. in the tree's understorey, with (apparently) negligible negative impacts on the host. In such cases which is the mediator organism: Is it the host? And should we still consider it plant facilitation – in this case, the parasite obtains resources from the host (a trophic interaction?) and then passes these to the understorey species. In terms of nutrient flows, is this not more akin to the action of grazers which by consumption of plant material and then defaecation on other plants benefit those plants through increased soil nutrient availability? What Watson's work certainly highlights is the need for studies with a large enough temporal or spatial scale to enable us to assess – in the round – the genuine nature of plant–plant interactions.

### So is it facilitation, and should we worry?

Why does it matter whether we know perfectly the nature of the balance of positive and negative interactions between

individuals? This is a theme that is specifically addressed in the article by Bronstein (2009). She argues that inconsistency in the definition of facilitation and a lack of assessment of the two-way nature of the interaction between beneficiary and benefactor are barriers in making links between mutualism and facilitation research despite the obvious potential that exists. The evolutionary impacts of facilitation may be quite different depending on whether the interactions are mutually beneficial, commensalistic or parasitic; and all of these reciprocal interactions have been documented. However, Bronstein argues, the reciprocal effects of facilitation are not investigated frequently enough to develop good models for the way in which facilitation might affect evolution. In addition, when considering the potential evolutionary impacts of facilitation, the traits acted upon are not well identified and neither are the fitness costs of facilitation commonly considered. Ultimately she argues that 'Filling these gaps should permit rapid progress in understanding how facilitation arises, persists and evolves'. This is critical, given the increasing evidence of the potential evolutionary impacts of facilitation.

Verdú *et al.* (2009) use molecular phylogenies to examine the role of facilitation in succession and community assembly and connect this to a series of recent phylogenetic studies of facilitation (Valiente-Banuet *et al.* 2006; Valiente-Banuet & Verdú 2007; Valiente-Banuet & Verdú 2008; Verdú & Valiente-Banuet 2008). They find that facilitation among distantly related lineages drives successional dynamics, but with a stronger element of phylogenetic determinism in facilitative interactions in Mediterranean communities. However, in drawing conclusions from such studies some assumptions concerning the underlying mechanism, no matter how convincing the data, are inevitable: field-based studies determining the mechanism of evolution (for example by examining facilitation's fitness costs, as suggested by Bronstein) are comparatively rare. To this end, theoretical, model-based studies have a lot of potential but both clear definitions and targeted field studies are essential.

### Don't worry, be happy

Throughout the papers discussed so far, we are faced with a clear question: precisely what does the term facilitation encompass? Some conceptual components are unique, such as those that challenge paradigms on the nature of communities. However, others clearly overlap fuzzily with other conceptual areas of research, as demonstrated throughout the papers in this Special Feature. We suggest that a simple way out of this dilemma is to take some guidance from competition research, from which many ideas about facilitation have emerged. Competition is a flexible concept and we are – on the whole – comfortable with this flexibility. In some instances, e.g. in conservation ecology, it is sufficient simply to focus on the target plant: is the species of interest suffering from competition that needs to be removed as part of the management process? In other instances, e.g. evolutionary modelling, greater specificity is required. In some cases, we are comfortable with discussing controlling factors broadly suggesting interference

and in others we are focused in particular on light, nitrogen or specific allelochemicals. However, we can also learn from competition research by noting the ongoing debates and difficulties in cross-study synthesis that can arise from a lack of clarity in defining the particular component of competition being addressed by a given study, or the use of inappropriate approaches. In facilitation research, we need to acknowledge that if we are working on the evolutionary impacts of facilitation, for example, we will have to go deeper than simply measuring its existence.

Having absolute definitions in ecology is always difficult. The vast array of interactions occurring in natural systems probably means that examples can be found (somewhere) that transgress the boundaries of definitions, but to keep broadly within the framework of existing facilitation research (and research in other arenas), we would suggest that direct beneficial trophic interactions between different groups of organisms should not be considered facilitation, but predation. Furthermore, Bronstein notes that 'few mutualisms involve species occupying the same trophic level', and so restriction of facilitation to within-trophic-level interactions may provide a scientifically reasonable distinction between these two processes. However, our boundaries obviously need to be flexible to include the host–parasite interactions described by Watson under the facilitation banner – especially if the ecological community as a whole can gain more insight into nature by doing so. Indeed, here we see feedback from facilitation research to other areas: should the mistletoe–host interactions described by Watson actually be defined as parasitism? This is as much a challenge to those researchers who work on parasitic plants as to those who work on facilitation. Similarly, Bronstein also notes that although those researchers interested in facilitation face the challenge of identifying 'features, both ecological and evolutionary, that unite diverse kinds of facilitation', we are not alone in that she also notes that 'The field of mutualism is taking on this same challenge'.

### Does any of it really matter?

Ecologists are sometimes accused of desipience – but is an interest in facilitation more frivolous than others in ecology? Probably not. In his keynote speech, Callaway (personal communication) discussed how integrating ideas generated from studies of facilitation have contributed to our understanding of biogeography, population and community ecology, ecosystems, evolution and conservation. Furthermore, and in addition to the work of Verdú and colleagues described above, three other papers in the Special Feature demonstrate the importance of facilitation processes for maintaining, regulating and restoring biodiversity in some environments.

Cavieres & Badano (2009) describe the community-level biodiversity impacts of cushion species along a latitudinal gradient in the Chilean Andes. In all the Andean plant communities that they studied, the presence of stress-tolerant cushion plants substantially increased the diversity of the entire community. Many species in some communities were found only within the cushions, and this is partly a consequence of cushion

plants increasing the altitudinal range of some species. Also considering the community-level implications of facilitation, Butterfield (2009) explores the effects of facilitation on temporal community dynamics, making a novel attempt to introduce facilitative interactions into models of plant communities. Butterfield shows that the impact of facilitation on community dynamics might be dependent on the mean or temporal variance of resource supply rates and stress levels. He finds that facilitative interactions can have both a stabilizing or destabilizing influence on dynamics, and these effects may also vary depending on the nature of the system being considered, e.g. herbaceous vs. woody-perennial vegetation, and the facilitative effect and response traits of the organisms involved. Finally, Gómez-Aparicio (2009) provides a wide-ranging review of the effects of facilitative interactions in ecosystem restoration. She argues that while the uptake of facilitation into ecological theory has been slow, its uptake into conservation practice has been even slower. She examines the types of system in which facilitation might be an important restoration tool, and points out the need to account for the possibility of temporal variation in its successful application (associated with ontogenetic shift in facilitative interactions).

Explicitly considering the role of facilitation in community organization has made substantial contributions to community theory, but examples from this Special Feature also demonstrate the broad importance of facilitative interactions in shaping the natural world as we know it. But perhaps, we are left with one further challenge: Can we now consider facilitation a conceptually independent research area? Although we believe that we can find a workable yet flexible definition for facilitation, are these conceptual areas already encompassed by other topics, such as plant competition, the evolution of mutualisms or the ecology of parasites? The argument in favour of developing a particular research field is that there is a substantial body of closely related topics that have not been previously or adequately addressed by other research areas and which are sufficiently distinct from them. We believe that this is currently the case for research on facilitation. With time and further exchange of ideas, we may find that research fields merge. Perhaps, for example, mutualism and facilitation will come together under a heading, such as 'beneficial interactions'. However, at present, although such fields are closely related and have substantial untapped potential to gain from each other, we are only at the start of breaking down these boundaries. Establishing facilitation as an independent concept has driven substantial progress towards a clearer understanding of the way in which ecological systems work (Callaway 2007). Not only will it continue to do this, but also we believe that as links to other conceptual areas in ecology and evolution solidify – aided, we hope, by the papers presented in this Special Feature and as a result of the benefits of integrating activities such as the BES Symposium – this progress will accelerate.

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